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ASPECTS OF ONTOGENY IN THE STUDY OF AMMONITE EVOLUTION

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It is well known that the development of an individual generally recapitulates to some extent the stages passed through during the evolution of its ancestors, or in other words, that "ontogeny repeats phylogeny." In the paleontological work of the last quarter of a century this principle of recapitulation has frequently been used in determining the relationships of fossils, and its general truth has been demonstrated among many groups of Invertebrates; for example, by Mr. R. G. Carruthers and others among the Rugose corals,[1] by Professor Grabau among the Gastropods,[2] and by numerous workers, particularly Mr. S. S. Buckman, among the Ammonites.[3]

That ontogeny is not always merely a recapitulation of phylogeny, however, has been recognized by zoölogists for many years; the development is often modified to fit the embryo for a special mode of life, as in many modern Arthropods, so that ancestral stages are obscured to a greater or less extent. In other cases on account of the individual hurrying through its development in order to attain maturity as early as possible, certain phylogenetic stages are "skipped" in development.

Numerous paleontologists have recognized the importance of this skipping of stages in development; Mr. S. S. Buckman dealt with it some years ago and has pointed out several examples.[4]

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[1] See, for instance, R. G. Carruthers, "The Evolution of *Zaphrensis delansuei*," *Quart. Jour. Geol. Soc.*, Vol. LXVI (1910), p. 523.

[2] A. W. Grabau, "Phylogeny of *Fusus* and Its Allies," *Smithsonian Misc. Coll.*, No. 1417 (1904), pl. xviii, fig. 2.

[3] See, for instance, "Yorkshire Type Ammonites." Introduction to Vol. I (1909–12).

[4] S. S. Buckman, "Monograph of the Inferior Oölite Ammonites," *Palaeont. Soc.*, p. 289.

More recently, he proposed to call it by the name of "saltative palingenesis";[1] Dr. W. D. Lang suggested the simpler term "lipogenesis"[2] but as this term may convey a wrong idea of the skipping of stages *in ontogeny*, Mr. Buckman has now proposed the term "lipopalingenesis."[3]

The study of fossil lineages affords a ready means of investigating the various ways in which the skipping of stages has been brought about. This is particularly true in the case of ammonites, among which it is comparatively easy to study the ontogeny of successive members of a lineage.

From such studies it appears that there are several slightly different ways in which phylogenetic stages come to be skipped in the development of later members of a series. The object in this article is to draw attention to some of these aspects of lipopalingenesis.

THE OMISSION OF EARLIER CHARACTERS

In many cases the characters omitted are those of the earliest ancestors, and the "skipping" means rather the omission of the earliest phylogenetic stages. This occurs as a direct result of the acceleration of development (tachygenesis). A simple example may be found in the evolution of the Ammonoids or Nautiloids. It is generally accepted that these have evolved from straight *Orthoceras*-like forms, through curved *Cyrtoceras*-like forms, to closely coiled forms like *Nautilus* itself. Now it may be admitted that the *Orthoceras*-like stage is repeated in an abbreviated manner, in the early portion of the *Cyrtoceras* form, but in succeeding members of the series this stage becomes progressively shorter, and in Mesozoic Ammonites it can scarcely be said to be represented at all.

In most cases of lipopalingenesis the stage or character omitted is not the most primitive.[4] This is illustrated by the skipping of certain ornament stages in the development of Ammonites. The normal order of appearance of ornamentation in Ammonites, as in many other groups is (*a*) striae, (*b*) costae, (*c*) tubercles. But although this order is followed in phylogeny almost invariably, and often, in a general way, in ontogeny, in certain "accelerated" members of phylogenetic series the striate and occasionally also the costate stages are omitted in development, the tuberculate stage having been accelerated so that it directly succeeds the smooth stage. The smooth embryonic stage of an Ammonite may be restricted to the first few whorls, but however accelerated the specimen, the inner whorls appear to be always smooth; the smooth stage is never skipped, while the later costate or striate stages may be.[1]

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[1] S. S. Buckman, "Yorkshire Type Ammonites," Vol. I (1909–12).

[2] W. D. Lang, *Proc. Geol. Assoc.*, Vol. XXX (1919), p. 60.

[3] S. S. Buckman, "Type Ammonites," Vol. III (1920), p. 11.

[4] It should be noted that in the case just given, the skipping of the *Orthoceras* stage merely represents the skipping of the earliest *skeletal* stage.

Similar examples may be found among the Brachiopods and Lamellibranchs. Dr. Lang points out to me that in certain advanced corals twelve septa appear simultaneously in the embryo, the early phylogenetic stages, with fewer septa, being skipped.[2]

THE OMISSION OF COMPARATIVELY LATE CHARACTERS

A more interesting form of lipopalingenesis is illustrated by certain Ammonite groups; perhaps the clearest example is to be found in the evolution of the Liparoceratidae.[3] Slender "capricorn" Ammonites of this family evolve through intermediate stages to stout bituberculate forms, but the ontogeny of the latter shows no stage in any way comparable with their immediate ancestors, the slender capricorn forms. This skipping of the slender-whorled stage is represented diagrammatically in Figure 1, which shows sections of three Ammonites typical of (*A*) the slender capricorn forms, (*B*) the intermediate forms, (*C*) the stout forms, from one genetic series. In the ontogeny of the capricorn form the depressed early whorls (i and ii) pass into round whorls (iii–v); in (*B*) the stage with depressed whorls is shortened (by acceleration of the slender whorl stage) but the latest whorls are stouter than in the adult of *A*. This stout form of whorl is more characteristic of *C*, and has been accelerated; since the depressed *early* whorls are also prolonged the slender whorl stage is skipped entirely in the development of this form.

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[1] In certain accelerated Gastropods striae may be present on the protoconch and the smooth stage is there omitted (Grabau, *op. cit.*).

[2] See *Geological Magazine*, N.S., Dec. V, Vol. IX (1912), p. 557.

[3] A. E. Trueman, "The Evolution of the Liparoceratidae," *Quart. Jour. Geol. Soc.*, Vol. LXXIV (1919), pp. 2, 7.

The reason for this skipping is perhaps best appreciated when it is remembered that the Ammonite *C* was thus able to produce the adult form directly, instead of developing from stout (embryo) to slender (youth) and back to stout (adult). The tendency to omit in development the stage which appears unnecessary for the production of the adult form would perhaps be expected; the most interesting fact is that this skipping is accomplished not simply by the acceleration of the stout form of whorl but partly by an *apparent* retardation of the early characters, notwithstanding that the series is distinctly progressive.

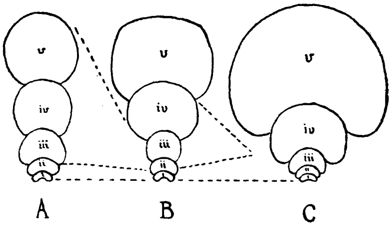

FIG. 1.—Sections to show the changes of whorl-shape in three ammonites from a single lineage of the Family Liparoceratidae:

A, a slender capricorn ammonite.

C, an involute stout ammonite.

B, a form intermediate between these two.

Without discussing here the biological interest of these observations, it is perhaps not out of place to notice that if lipopalingenesis is of frequent occurrence, the tracing of phylogeny from ontogenetic evidence is not so easy as has been thought by some workers. It is comparatively easy to follow cases of skipping of stages when an early phylogenetic stage is omitted, but in cases like the one just described, where the characters omitted are some of the more advanced, there is obviously much difficulty in tracing descent from developmental evidence alone. In such cases, descent can only be proved by the finding of series of intermediate forms connecting the various species.